CHAPTER 3

Parental provisioning behaviour predicts survival of Cape gannet chicks under poor conditions

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Abstract

Cape gannets (*Morus capensis*) are declining in numbers in all breeding colonies at the southern African west coast, potentially caused by deteriorating food availability. The behavioural responses of individuals to changing conditions can provide insights into the mechanisms that drive population dynamics. We studied the relationship between parental provisioning behaviour and the breeding success of Cape gannets breeding at Ichaboe Island (Namibia) in two years with different nesting success, to assess the potential role of variation in food availability in explaining variation in chick survival. In 2006/07 parents delayed the onset of breeding and visited nests at a lower frequency than in 2005/06, indicating that food availability was limited. Within the years individual differences in provisioning rate but not in parental condition were associated with chick growth and survival. These positive associations remained present when controlling for seasonal changes. Predation, not starvation, was the main cause of mortality. Under poor conditions, as indicated by long foraging trips, Cape gannet parents left small chicks unattended, resulting in many being killed by kelp gulls *(Larus dominicanus*). Long foraging trips were associated with reduced average breeding success, but impacted some parents more than others. Knowledge of the origin of this inter-individual variability is needed to predict how changes in food availability affect seabird population dynamics, which is one of the steps towards conservation of these birds.

INTRODUCTION

Seabird population dynamics are often linked with their food supply (Sinclair 1989). Numbers of breeding Cape gannets (*Morus capensis*) in the Benguela ecosystem, off the western coast of southern Africa, have been declining over the last few decades due to changes in the abundance and distribution of their epipelagic fish prey anchovies (*Engraulis encrasicolus*) and sardines (*Sardinops sagax*) (Crawford *et al.* 2007*a*). The decreased availability of these lipid-rich prey species affected both the foraging effort of parents (Lewis *et al.* 2006, Pichegru *et al.* 2007) and growth of the chicks (Batchelor & Ross 1984, chapter 2).

Seabirds breed in a patchy and unpredictable environment (Ashmole 1963) and during the breeding season they potentially encounter both temporal and spatial fluctuations in prey distribution. Flexibility in foraging behaviour is expected (Erikstad *et al.* 1998) and selection favours those behavioural responses that maximize fitness, especially when food is scarce (Goss-Custard & Sutherland 1997). Chick growth and survival partly depend on parental behaviour. Decreased provisioning rates (Gray & Hamer 2001, Le Corre *et al.* 2003) and food loads (Weimerskirch *et al.* 1997*a*) or reduced quality of prey species (Litzow *et al.* 2002) negatively affect chick growth and survival. Nest attendance is important for young chicks that need brooding or protection against predators (Nelson 1978). The possibility to increase the rate of food provisioning is partly determined by food availability around the breeding colony (Jarvis 1974 vs. Navarro 1991), but may also be related to phenotypic differences between parents. Handicapping experiments have shown that there is individual variation in the extent to which seabird parents can increase their reproductive effort (Velando 2002, Paredes *et al.* 2005).

We studied the relation between parental behaviour and breeding success in the Cape gannet at Ichaboe Island (Namibia) during two years. Cape Gannets are qualified as 'vulnerable' by IUCN (IUCN 2007). Ichaboe houses the largest Cape gannet colony in Namibia (approximately 8700 breeding pairs, Crawford *et al.* 2007*a*). In 2006/07, Cape Gannets delayed breeding by approximately 6 weeks compared to 2005/06. Cape fur seals (*Arctocephalus pusillus pusillus*) suffered increased starvation and an increase in spontaneous abortions in 2006/07, and Cape cormorants (*Phalacrocorax capensis*) abandoned two breeding attempts before they actually commenced breeding three months later than previous years (T. Delport, pers. comm.). We take these observations as an indication that food availability was poor around the breeding colony in 2006/07 compared to 2005/06. In this paper we study the link between behaviour and body condition of Cape gannet parents and growth and survival of the chicks, to assess why some parents manage to rear their offspring, whereas others do not. This might give some insights in behavioural mechanisms associated with population dynamics. We predict that 1) chick growth and survival

are low in years with long foraging trips and that 2) parents with longer foraging trips have lower breeding success.

METHODS

The study was conducted at Ichaboe Island, Namibia (26°29'S, 14°94'E) during four periods in the breeding seasons of 2005/06 and 2006/07: December 2005 = 16 December 2005 to 20 January 2006; February 2006 = 23 February to 12 March 2006; December 2006 = 21 December 2006 to 5 January 2007; February 2007 = 8 February to 4 March 2007. The breeding season was divided into early (December 2005 and 2006) and late periods (February 2006 and 2007), indicated as half-seasons in statistical models. Gannets had delayed their breeding in 2006/07, so we only found 14 chicks at the study site in December 2006.

Marking and behavioural observations

In each study period we selected nests within 1 m from the periphery of the colony with chicks of variable ages (49 nests in December 2005, 33 in February 2006, 14 in December 2006 and 41 in February 2007). Selecting nests in the interior of the colony would cause disproportional amounts of disturbance. Cape gannets at the fringes are similar in age and quality as birds in the interior (Klages 1994), so no biases in behaviour are expected, neither in chick growth (chapter 2).

At each selected nest we captured the parents from their nest by manipulating a hooked pole around their neck. Gannets were then measured (bill length to the nearest 0.1 mm, length of flattened wing chord to the nearest mm and body mass to the nearest 25 g) and dyed with picric acid. Our measuring routine differed slightly between the two years. In 2005/06 we measured and dyed the adults of the selected nests in the morning to obtain pre-feeding morning mass. In 2006/07 adults were marked in the afternoon without capture using a marker tied to a stick and we took measurements the next morning if the adults were still present at the nest. Partners were captured and measured within four days after the capture of the first parent, again after they spent the night on the nest to obtain the closest estimate of pre-feeding mass. Each study nest thus had individually recognisable parents; one dyed on the back, the other either had a colour ring or was dyed on the head.

Nest attendance at each nest was recorded by checking nests every hour from sunrise to sunset (5 AM to 8 PM, Namibian summer time). Gannets are visual hunters and therefore do not forage at night (Ropert-Coudert *et al.* 2004*b*). If a different parent was observed attending the nest in the morning than on the previous night, we assumed that the nest relief happened shortly after sunset. We calculated several variables from the observational data: (1) hours away from nest (trip duration), (2)

hours on the nest (attendance bout), and (3) average number of foraging trips per day (trip frequency).

The Cape gannet is a monomorphic species, so sexes could not be distinguished in the field. Therefore we collected some feathers of one bird per nest for later sex determination through DNA analyses (see Fridolfsson & Ellegren 1999 for detailed methods). To verify the sexing method we collected feathers from both parents of 10 nests. All pairs consisted of two sexes.

Chick growth

We measured bill and wing length of study chicks at 5–7-day intervals. Body mass was measured to the nearest 5 g (<1 kg) or 25 g (>1 kg) with Pesola spring balances. Each date, we weighed chicks at fixed times and in the same sequence. Chicks were fitted with colour rings after 3–4 weeks, depending on tarsus size. Chick age was estimated from the first measurement of each chick, using algorithms derived from 103 known aged chicks from Navarro (1991). If wing length was < 40 mm, age was computed by $age = -\ln((89.78 - b / 6.15 \times b) / 0.086) + 0.5$ days, where b is bill length in mm. For chicks with wings ≥ 40 mm, age was computed by $age = 1.395 - \ln(\ln(588.8 / w) / 0.0264) + 0.5$ days, where w is wing length in mm. Age was then calculated by adding the actual number of days that passed since the first measurement. We calculated growth indices (z-scores) from the mass increments of each chick, as departures from average growth (Box 2.1). This growth index is independent of chick age. For each interval we averaged growth indices for all chicks from the study nests. In total we obtained growth data for 132 chicks (n = 47, 12, 40 and 33 for each study period respectively) from which we calculated 434 growth indices.

Survival was calculated as daily survival rate, to correct for differences in length of the observational periods, and expressed as weekly survival rates. Chicks that did not survive were assigned to one of three categories; 1) died without being predated (called starved), 2) taken while at least one parent was present at the nest (predated) or 3) died of weather conditions or predated while no parent was present at the nest (abandonment). We cannot exclude the possibility that "starved" chicks died from other causes (for example from a virus infection).

Statistical analyses

Results are presented as mean ± standard deviation. We have no sex-specific data on parental behaviour in February 2006. Therefore we first present the averages of the behaviours, body condition and chick growth for all four periods and then look in more detail into the three study periods of which we do know the sexes of the adults. Chick survival was analysed using a logistic regression. Multilevel models were used to take repeated measures and dependent observations into account for chick growth (individual and observation as levels) and parental behaviour (nest, individual and

observation as levels). Significance levels were calculated with restricted iterative generalized least squares (RIGLS). Body mass divided by wing length was used as an index of body condition (Lewis *et al.* 2006) and regressed on the onset of breeding (Linear regression: chick age $r^2 = 0.08$, $F_{1,193} = 16.6$, $P < 0.001$), after which we used residual body condition. During the three study periods for which we know the sex of each adult, we collected data from 204 different birds, concerning 2482 foraging trips and 2380 nest attendance bouts. Behavioural response variables were ln-transformed. Average chick age differed between the study periods (One-way ANOVA $F_{3,123} = 22.3$, $P < 0.001$, Table 3.1) and was included as a covariate in statistical models exploring parental behaviour. All multilevel models included sex and study period ($n = 3$) as factors and chick age as a covariate. To test the relationship between parental behaviours and chick growth or survival, we either averaged (trip duration and attendance bouts) or summed (trip frequency) behaviours for both sexes per nest for the same intervals as the growth increments, so parental behaviour and chick growth could be related to each other for the same period. Included in these models were study period as a factor and chick age and behaviour (attendance bout and trip frequency) as covariates. The models that looked at the association between parental behaviour and chick growth or survival were compared by calculating the Deviance Information Criterion (DIC). This is a generalisation of the Akaike Information Criterion (AIC), derived through Markov Chain Monte Carlo (MCMC) methods, and used to compare multi-level models. Models with the lowest DIC fit best, as with the AIC (Spiegelhalter *et al.* 2002).

Table 3.1. Mean age (SD) of Cape gannet chicks and mean mass and body condition (mass/wing length) of parents per sex at the beginning of each study period in 2005/06 and 2006/07.

	Chicks		Females			Males		
	Age (d)	*n*	Mass (g)	Condition	*n*	Mass (g)	Condition	*n*
December 2005	19.6 (10.4)	47	2636 (221)	5.67 (0.43)	44	2524 (256)	5.43 (0.55)	48
February 2006	41.9 (18.3)	33						
December 2006	8.1 (6.7)	14	2700 (167)	5.68 (0.36)	14	2621 (220)	5.49 (0.46)	14
February 2007	22.3 (12.3)	40	2541 (164)	5.37 (0.34)	34	2482 (165)	5.32 (0.35)	37

RESULTS

Chick growth and survival

In 2005/06 chick growth increased from 19 December until 9 January, then decreased (Fig. 3.1). At the end of February growth rates were similar to those of January, but they decreased in the last two weeks of the study period. In 2006/07 chick growth rates in December were within the range of growth the year before (Fig. 3.1). In February growth was slower than earlier in that year and decreased even more in the last week, but it was similar to growth in the year before at that time. Chick growth differed significantly between years and weeks (Multilevel model: year $\chi^2 = 7.1$, $P = 0.008$; week $\chi^2 = 57.3$, $P < 0.001$) and decreased during both years (Multilevel model: year n.s.; season half $\chi^2 = 24.6$, $P < 0.001$; interaction n.s.).

Weekly survival of the study chicks was better in 2005/06 than in 2006/07 (98.8% and 92.6% respectively). In 2005/06 weekly survival of the study chicks was constant and high throughout the breeding season; 98.8% in both study periods. In 2006/07 survival decreased from 97.0% in December to 90.8% in February. Survival tended to be higher early in the breeding season, but not significantly so (98.4% in December and 94.7% in February, Logistic regression: year $\chi^2 = 15.8$, $P < 0.001$; season half $\chi^2 = 3.2$, $P = 0.072$, interaction n.s.). Survival was lower for chicks with slow growth rates and of younger age (Logistic regression: growth $\chi^2 = 7.2$, $P = 0.007$; chick age $\chi^2 = 38.9$, $P < 0.001$). The average age at which chicks died was 25.9 days (± 9.2, $n = 23$, range 14 – 56).

Parental body condition

The initial body mass of adults did not differ between years (2005/06: 2580 g ± 247.0, $n = 140$; 2006/07: 2552 ± 186.1, $n = 105$) and was lower at the end of 2006/07 (GLM: chick age n.s.; year n.s.; season half $F_{1,239} = 5.1$, $P = 0.025$; year x season half F1,239 = 6.0, $P = 0.015$). Wing length was longer in 2006/07 compared to 2005/06, but decreased from early to late 2006/07 (GLM: year $F_{1,237} = 33.7$, $P < 0.001$; season half $F_{1,237} = 6.1$, $P = 0.014$; interaction $F_{1,237} = 4.7$, $P = 0.031$). Body condition (mass/wing length) did not differ between the two breeding seasons, but was significantly lower later in the year. Female body condition was on average 6.45% greater than male body condition (Table 3.1) and body condition decreased with increasing chick age (GLM: year n.s.; sex $F_{1,187} = 6.5$, $P = 0.012$; season half $F_{1,187} = 5.4$, $P = 0.021$; chick age $F_{1,187} = 11.9$, $P = 0.001$).

Parental behaviour

As we do not know the sexes of the parents in February 2006, we first compared the average behaviour of all birds with the means of February 2007. Foraging trips were 6 h shorter in February 2006 compared to February 2007 (28.2 and 34.3 h respectively,

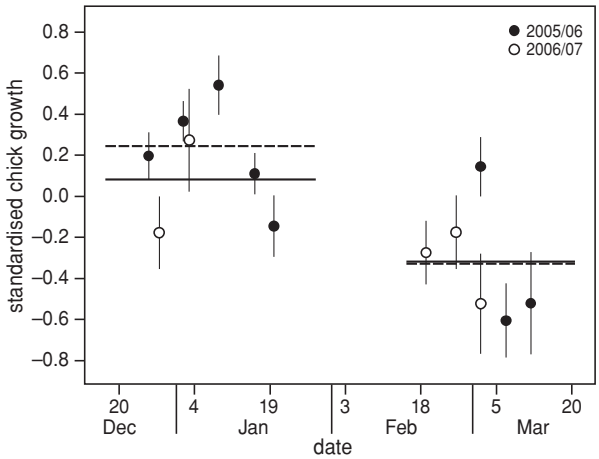

Figure 3.1. Mean standardised Cape gannet chick growth and standard errors for each interval (4–7 days). The lines represent the mean growth per study period.

Multilevel model: $\chi^2 = 8.5$, $P = 0.003$) and birds stayed 5 h shorter on the nest (16.3 and 21.4 h respectively, $\chi^2 = 20.1$, $P < 0.001$).

In the three study periods with parents of known sex, both trip duration and attendance bouts decreased with increasing chick age, so nest visitation rates increased when chicks became older (Table 3.2). Females made longer trips and shorter attendance bouts than males and consequently males had higher nest visitation rates (Fig. 3.2, Table 3.2). In February 2007 (the year for which we have sex-specific data), trip durations of female gannets were elevated by 59% compared to the

Table 3.2. Multilevel mixed-models testing the main effects on parental behaviours of Cape gannets in 2005/06 and 2006/07. Coefficients (B) indicate direction of effects, relative to the reference category. Weeks coincide with growth interval of the chicks.

		A) Trip duration (h)			B) Attendance bout (h)			C) Trip frequency (per d)		
	df	*B (SE)*	χ^2	*P*	*B (SE)*	χ^2	*P*	*B (SE)*	χ^2	*P*
Intercept	1	3.26 (0.07)	1974.8	< 0.001	3.40 (0.07)	2584.9	< 0.001	–1.13 (0.06)	380.2	< 0.001
Sex[a]	1		40.9	< 0.001**		5.5	0.020*		28.9	< 0.001**
males		–0.32 (0.05)			0.09 (0.04)			0.15 (0.03)		
Week	8		64.3	< 0.001**		30.8	< 0.001**		104.4	< 0.001**
Chick age	1	–0.01 (0.002)	14.2	< 0.001**	–0.03 (0.002)	151.0	< 0.001**	0.01 (0.002)	37.6	< 0.001**

[a]reference category is females

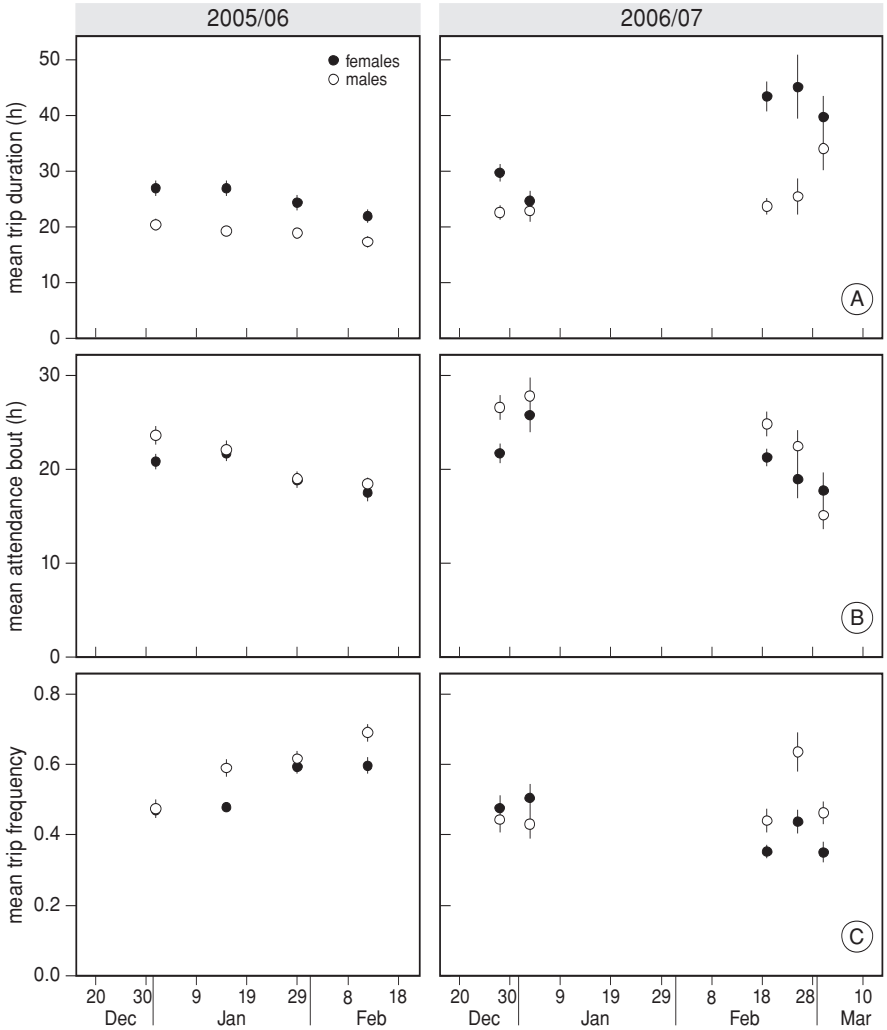

Figure 3.2. Sex-specific means and standard errors of A) trip duration, B) attendance bouts, and C) trip frequency of Cape gannets for two study years. No sex-specific data were available for the second half 2005/06.

mean of December 2006 (December 2006: 27.0 ± 10.4, n = 66; February 2007: 43.6 ± 38.9, n = 280) and were 17.5 h longer than male trip duration (males: 26.1 ± 26.2, n = 370). Male trip duration increased to 33.9 h in the last week. The sex differences in trip frequency were not constant between weeks. Male gannets increased their trip frequency faster with increasing chick age than females (Multilevel model: sex x weeks $\chi^2 = 10.4$, $P = 0.001$; sex x chick age $\chi^2 = 20.7$, $P = 0.008$).

Chick growth in relation to parental behaviour and body condition

Parental trip duration was highly correlated with trip frequency (Pearson r = -0.617, P < 0.001) and we therefore only looked at the association between chick growth and trip frequency or attendance bouts. Attendance bouts and trip durations were positively correlated between the sexes (Bivariate correlations: attendance bout r = 0.540, P < 0.001; trip duration r = 0.334, P < 0.001).

The model with trip frequencies separated per sex showed that paternal trip frequency was associated with chick growth, but maternal trip frequency was not (Multilevel model: maternal trip frequency *B(SE)* = 0.24(0.17), χ^2 = 2.0, P = 0.155; paternal trip frequency *B(SE)* = 0.44(0.17), χ^2 = 6.8, P = 0.009, DIC 756.6). The model that best explained the association between chick growth and trip frequency combined the trip frequency for both sexes: chick growth was positively associated with the number of parental nest visits (Table 3.3, DIC 755.7). Variation in attendance bouts was not associated with variation in chick growth in any of the models (Table 3.3).

Chick growth in the first week after measuring parental body condition was positively associated with residual maternal body condition (Linear regression: residual maternal body condition $F_{1,86}$ = 4.3, P = 0.042). When study period was included in the model the association between chick growth and maternal residual body condition was not significant (GLM: residual maternal body condition n.s.; study period $F_{2,84}$ = 3.5, P = 0.035). Both parental and paternal residual body condition were not associated with chick growth, neither in any of the models with residual body mass instead of residual body condition.

Table 3.3. Multilevel mixed-models testing the main effects on Cape gannet chick growth for behaviour of both parents combined in 2005/06 and 2006/07. Parental behaviours are attendance bout (h), and trip frequency (d^{-1}). Coefficients (B) indicate direction of effects, relative to the intercept. Study periods indicate the three periods in which the sex of the parents is known in 2005/06 and 2006/07.

		Attendance bout (h)			Trip frequency (per d)		
	df	*B (SE)*	χ^2	*P*	*B (SE)*	χ^2	*P*
Intercept	1	0.47 (0.72)	0.42	0.515	0.53 (0.15)	11.90	< 0.001
Study period	2		29.89	< 0.001		15.77	< 0.001**
Chick age (d)	1	–0.01 (0.005)	1.18	0.277	–0.01 (0.005)	7.34	0.007**
Parental behaviour	1	–0.03 (0.19)	0.023	0.879	0.65 (0.21)	9.65	0.002**

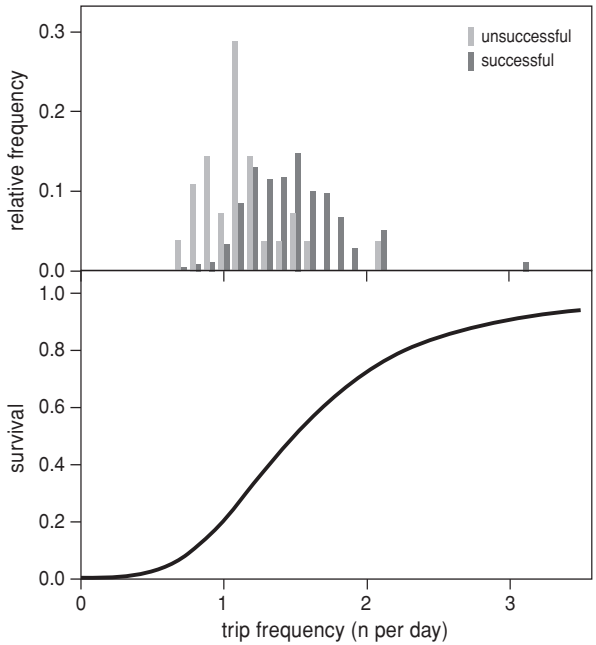

Figure 3.3. Survival of Cape gannets as a function of trip frequency by logistic modelling. The top panel gives the frequency distribution for successful and unsuccessful nests as fraction of total per category.

Chick survival in relation to parental behaviour and body condition

Chick survival was reduced when parents visited the nests less frequently (Fig. 3.3, Table 3.4A). Chick survival was significantly associated with maternal trip frequencies (B(SE) = 2.34 (1.0), $\chi^2 = 5.51$, $P = 0.019$), but not with paternal trip frequency (B(SE) = 1.49 (0.9), $\chi^2 = 2.59$, $P = 0.107$). Despite the positive correlation between the trip frequencies of both sexes, the model with only maternal trip frequency showed the lowest DIC (0.43 vs. 0.58 for the parents combined).

The best model explaining variation in chick survival from variation in attendance bouts was the model with the behaviour of the sexes separately; when males had increased attendance bouts their chicks had lower survival chances (Table 3.4B, DIC 0.74), but there was no association with maternal attendance bouts. The estimates of the sexes differed in direction, indicating different consequences of parental behaviour for chick survival. Also when tested in separate models, paternal attendance bouts were associated with chick survival (Multilevel model: B(SE) = -2.44 (1.1), $\chi^2 = 5.40$, $P = 0.020$), whereas maternal bouts were not (Multilevel model: B(SE) = 0.46 (0.65), $\chi^2 = 0.51$, $P = 0.477$).

Survival of chicks was not associated with either parental or paternal residual body condition, but tended to be reduced if maternal residual body condition was reduced as well (Logistic regression: residual maternal body condition: $\chi^2 = 3.8$, $P = 0.051$). None of the models that included study period showed any significant association between chick survival and residual body condition and residual body mass of parents combined or separated.

Table 3.4. Multilevel mixed-models testing the main effects on Cape gannet chick growth for behaviour of both parents combined in 2005/06 and 2006/07. Parental behaviours are attendance bout (h), and trip frequency (d^{-1}). Coefficients (B) indicate direction of effects, relative to the intercept. Study periods indicate the three periods in which the sex of the parents is known in 2005/06 and 2006/07.

		Attendance bout (h)			Trip frequency (per d)		
	df	*B (SE)*	χ^2	*P*	*B (SE)*	χ^2	*P*
A							
Intercept	1	11.23 (4.92)	5.23	0.022	2.85 (1.41)	5.22	0.022
Study period	2		16.74	< 0.001**		14.31	0.001**
Chick age (d)	1	0.09 (0.04)	3.88	0.049*	0.12 (0.04)	12.61	< 0.001**
Parental behaviour	1	–2.53 (1.29)	3.84	0.050*	2.99 (1.26)	5.61	0.018*
B							
Intercept	1	9.14 (4.59)	3.97	0.046	5.04 (1.82)	7.64	0.006
Study period	2		15.72	< 0.001**		13.07	0.001**
Chick age (d)	1	0.11 (0.05)	5.91	0.015*	0.14 (0.04)	12.51	< 0.001**
Maternal behaviour	1	0.70 (0.78)	0.80	0.370	2.24 (1.04)	4.62	0.032*
Parental behaviour	1	–2.63 (1.09)	5.89	0.015*	1.12 (0.98)	1.29	0.256

Table 3.5. Weekly survival rates of Cape gannet chicks from Ichaboe during 2005/06 and 2006/07. The three causes of death of our study chicks and their absolute and relative contribution to the number of mortalities in each study period are indicated.

	n	Weekly survival	Starvation	Predation	Abandonment
December 2005	49	98.8%	3 (100%)	0	0
February 2006	33	98.8%	0	2 (100%)	0
December 2006	14	97.0%	0	2 (100%)	0
February 2007	41	90.8%	1 (6.25%)	4 (25%)	11 (68.75%)
Total	137	96.5%	15.4%	30.8%	53.8%

Nest absences and predation

We could not statistically demonstrate that the level of parental non-attendance was associated with chick survival. We do have several indications, however, that attendance is important for chick survival. In February 2007 chicks were left alone by the parents after which they either died of cold temperatures (4 cases) or were predated by kelp gulls (7) (Table 3.5). Chicks younger than 30 days that were left alone were usually killed by kelp gulls within a few hours. For two "predated" chicks we do not know whether they were abandoned and then predated, or were predated and then the attending parent left. Chicks that did not survive were left unattended for the first time when they were on average 10 days younger than surviving chicks (21.2 and 31.6 d respectively, One-Way ANOVA: $F_{1,52} = 32.2$, $P < 0.001$).

DISCUSSION

We studied behavioural responses of Cape gannets to changes in their prey environment and associated this behaviour with growth and survival of their offspring. The duration of foraging trips of breeding gannets increased from 2005/06 to 2006/07, indicating a decrease in food availability between these breeding seasons. The provisioning rates to the chicks and the level of attendance decreased in 2006/07, as did chick growth and survival. Chicks were left alone at a younger age and became vulnerable for weather condition and predation. Predation of chicks by kelp gulls increased in 2006/07 and impacted strongly on the survival of chicks in the colony. When foraging trips were on average long, parental behaviour was directly associated with chick growth and survival likely due to reduced provisioning rates, but also through increased predation on chicks that were left unattended.

Chick growth and survival

Unfortunately, no data on food availability in the Namibian waters were available, so we could only derive indirect estimates of changes in food availability. When foraging conditions become poorer, trip durations and foraging ranges of breeding animals increase concomitantly (Boyd *et al.* 1994, Suryan *et al.* 2002, Kowalczyk *et al.* 2006). The longer foraging trips in 2006/07 compared to 2005/06 would suggest lower food availability around Ichaboe in 2006/07. This interpretation is consistent with the delayed onset of breeding by both Cape gannets and Cape cormorants in 2006/07.

The longer foraging trips in 2006/07 were associated with slower chick growth and decreased survival in 2006/07 compared to 2005/06. Within both years chick growth decreased during the breeding season. In the first year the reduced growth was not associated with decreased survival rates, which remained high throughout

Photo 3.1

the year (98.8%). In February 2007 however, the weekly survival rates decreased with 8%, which was associated with slower chick growth, but also with reduced provisioning rates of the parents. The decreased growth and survival rates of the chicks in concert with the increased foraging trip duration of the parents in 2006/07 suggest adverse changes in the environment like food shortage during which parents could not sustain the increasing energy demands of their offspring.

Sex-specific foraging behaviour

In Cape gannets the parental behaviours of both sexes were positively correlated, but averaged over two years, males made considerably shorter foraging trips (21.1 h) and visited the nest more often (0.56 visits per day) than females (29.7 h trips; 0.48 visits per day). In the closely related northern gannets (*Morus bassanus*) the sexes do not differ in trip duration, but females make longer and deeper dives and spend more time at the sea surface than males (Lewis *et al.* 2002). The differences in foraging behaviour may suggest different roles for the sexes. Longer foraging trips of female gannets may indicate that they explore different feeding grounds (Weimerskirch 1993, González-Solís *et al.* 2000, Weimerskirch *et al.* 2006), thereby possibly reducing intra-specific competition at the feeding sites near the colony (e.g. Hunter 1983).

During the presumed deterioration of the food situation, female gannets increased their trip duration by 59%, several weeks before the males increased theirs. The

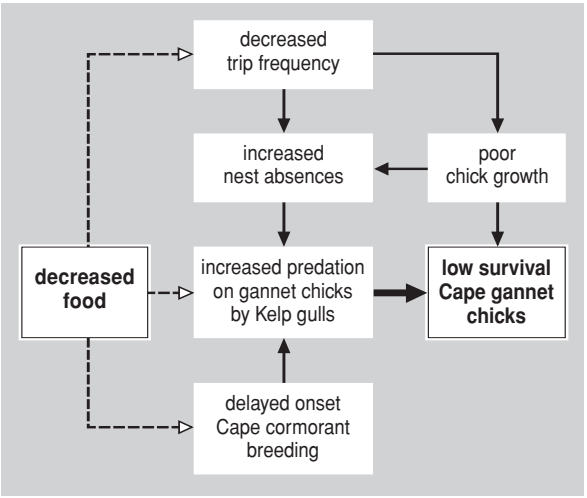

Figure 3.4. Behavioural diagram showing the interactions between food availability, parental behaviour and chick growth and survival of Cape gannets and the dynamics with other seabird species. We have no direct data on food availability (hence the dashed arrows), but strong evidence that food availability drives these processes.

decreased provisioning rates of both parents affected chick growth, but only the reduced trip frequencies of mothers were positively associated with chick survival. Foraging strategies should maximize the chances of finding local sites of high food availability in order to minimize the energetic costs of foraging (Parrish *et al.* 1998). If good quality prey shifts to more distant sites, females possibly attempt to follow such prey and increase trip duration. Males responded by staying longer at the nest with the chick, hence the association between male attendance bouts and chick survival. Short intervals between consecutive feedings and the regularity of food deliveries are important in optimizing seabird chick growth (Schaffner 1990, Weimerskirch *et al.* 2000*b*, Gray & Hamer 2001). Only in nests where females managed to keep their trip frequency high, the offspring managed to survive. The evolutionary significance of sex-differences in foraging behaviour in monomorphic species like the Cape gannet remains a puzzle (Lewis *et al.* 2002) and we need at-sea data to look into this more specifically.

Parental behaviour, chick growth and survival

We suggest the following scenario for the two breeding seasons in which we collected data, based on our field experience and our results (Fig. 3.4). Under favourable conditions in 2005/06 (shorter foraging trips and higher chick growth rates and survival) both sexes increased their provisioning rates when the chick became older to sustain

increasing chick energy demands. When conditions were less favourable in 2006/07, female gannets substantially increased their trip duration. Consequently males had to stay longer at the nest when chicks were at an age that they still needed brooding for thermoregulation or protection against predators. As a result the total provisioning rate to the chick declined and chicks showed reduced growth rates and survival. Cape cormorants normally breed in large numbers on Ichaboe Island (Crawford *et al.* 2007*b*). Kelp gulls mainly predate cormorant eggs, paying little attention to gannets. In 2006/07 the Cape cormorants delayed breeding, most likely due to decreased food availability. This led to kelp gulls increasing their predation pressure on the gannets. Gannet parents with young chicks had two options; either stay at the nest to protect their chick, which then had increased chances to starve, or leave their chicks to increase provisioning rates, giving kelp gulls the opportunity to predate their offspring. From our data it appeared that gannet parents left their chicks to increase food intake, apparently not to jeopardize their own survival (Williams 1966). This mechanism is also found in Arctic skuas (*Stercorarius parasiticus*) (Davis *et al.* 2005); low food availability forced skuas to increase their foraging effort and decrease attendance rates, which in turn increased the predation pressure by great skuas (*Catharacta skua*).

Conclusions

Cape gannets breeding in the Benguela ecosystem are limited in their foraging behaviour by food abundance and it was suggested that gannets are foraging at their energetic boundaries (Lewis *et al.* 2006, Pichegru *et al.* 2007). We found that parental body condition did not differ between the years, indicating that even when food conditions were poor parents remained at similar body mass as in favourable years. In this way, allocation decisions in poor years favoured the survival of parents above increased foraging effort for the young. This parental response seemed the underlying cause of the reduced reproductive output of the whole breeding colony in poor foraging years. Conservation measures in the breeding colonies, by actively keeping kelp gulls away from Gannet nests, would therefore be insufficient to enhance the breeding success of Cape gannets. If local food availability does not improve, the decline in Cape gannet population numbers is unlikely to reverse.

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